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Tree Water Status Affects Induced Southern Pine Beetle Attack and Brood Production

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SUMMARY

Artificially induced moisture stress lowers loblolly pine resistance to attack by the southern pine beetle. The duration of oleoresin flow is curtailed and egg laying and larval development can progress rapidly.

Tests conducted from 1973 through 1975 involved artifically induced beetle attacks with limited populations. Even beetles that attacked first met little resistance in stressed trees.

Although beetles can successfully attack the healthiest loblolly pines, unstressed trees in the study resisted initial attack. Prolonged oleoresin flow entrapped or pitched out many beetles and delayed egg laying and larval development.

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Observations by foresters and entomologists indicate that moisture stress increases a tree's susceptibility to attack by the southern pine beetle, *Dendroctonus frontalis* Zimm. (Thatcher 1960). Vite (1961) reported that bark beetle success is correlated with low oleoresin exudation pressure (OEP), and change in OEP is directly related to water stress in *Pinus ponderosa* Laws. With large loblolly pines (*Pinus taeda* L.), artificially induced moisture stress has marked effects on OEP and the relative water content of the inner bark (Lorio and Hodges 1968). The study reported here further examines the relationship between host tree physiology and the success of southern pine beetle (SPB) attack.

MATERIALS AND METHODS

Loblolly pines in natural stands were used for the study. First attempts at inducing beetle attacks were conducted in summer 1973 in the lower West Gulf Coastal Plain with sawtimber-size trees. The area had a native population of southern pine beetles.

Three pairs of trees were selected. Each pair had one prematurely declining and one apparently healthy tree. Following a method of T. L. Payne and J. E. Coster (personal communication), trees were rigged with 30-cm square hardware cloth traps coated with Stickem Special®[1] Traps were placed at 0.6, 2.4, 4.2, and 6.0 m above ground level on one side of the tree and at 1.2, 3.0, and 4.8 m on the other side. A pulley system was used to lower traps for daily inspection and collection of beetles.

One pair of trees was used at a time. Loblolly pine bolts artificially infested with male-female pairs of beetles were used as attractants. These bolts were removed once a mass attack was established. When brood developed to the late larval or pupal stage, trees were felled and a 15-cm and a 30-cm bolt were taken between the 3.7 to 4.9 m levels. The longer bolts were placed in rearing cans so that emerging beetles could be counted. The shorter bolts were dissected and successful attacks counted. Emergence divided by 2 times the number of successful attacks provided an estimate of the ratio of increase of brood over successfully attacking adults (Thatcher and Pickard 1964).

To avoid large beetle populations, a second test (1973) was located on the upper West Gulf Coastal Plain in a dense loblolly pine stand that was apparently free of SPB. Trees averaged 20 cm in diameter at breast height (dbh) and 18 m in height. There was no evidence of declining trees. Moisture stress was induced in two trees by digging a narrow trench 1 m deep at a radius of 2 m around each tree. Trenches were lined with 6-mil polyethylene and refilled with soil. Shelters of exterior plywood covered with roofing felt were built around the trees and beyond the outer edge of the trenches to prevent soil water recharge. Two untreated study trees were used as controls.

In this test, attacks were induced with vials containing approximately 1 ml of synthetic attractant (Frontalure®) placed 4.3 m above ground on each tree. Attacking beetles came from naturally infested loblolly pines in the lower Coastal Plain. Approximately fifteen 60-cm bolts containing callow adults were placed around each tree. Sticky traps were used to assess attack patterns.

Two subsequent tests were established, one in 1974 and one in 1975. These tests were again conducted in an upper Coastal Plain area with no known SPB infestations. Three pairs of trees were used in 1974 and one pair in 1975. Moisture stress was induced in one tree in each pair and the other was used as a control. Trenches and shelters were constructed as before. Trees averaged 28 cm dbh and 15 m tall in 1974 and 30 cm dbh and 19 m tall in 1975.

[1]Trade names and company names are included to identify equipment and materials used and do not constitute endorsement by the USDA.

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Aluminum access tubes were installed to allow measurement of soil moisture with a neutron probe. Shelters were completed and soil moisture measurements begun by 17 May 1974 and 21 May 1975. Measurements were taken weekly with a modified Kaiser soil moisture probe (Model VMP 487) and a Troxler Scaler (Model 1651) 1 m from the bole and 25, 40, 55, 70, 85, 100, and 115 cm below the soil surface.

Sticky traps were not used in the 1974 or 1975 tests. Attacks were again induced with snythetic attractant and naturally infested bolts containing callow adults. When 15 to 25 attacks were observed near the attractant, vials and bolts were removed and the beetles destroyed to ensure a limited attack.

Bark samples were taken to assess attacks and brood development at 1.8, 3.6, and 5.5 m. One-tenth square foot samples were taken with an electric-powered hole saw from two sides of the tree 2 to 4 weeks after attack. Sampling varied according to our subjective judgement of attack progress.

Measurements of tree physiological status included OEP and oleoresin flow over a 24-hour period. OEP was measured as described by Hodges and Lorio (1968). Xylem water potential of twigs was estimated on three trees in August 1974 when it was evident that a wide difference in the water status of trees existed. The pressure-chamber method of Scholander *et al.* (1975) was used.

RESULTS

1973 Tests: The first test compared declining trees with apparently healthy trees in the lower Coastal Plain. The attraction technique was successful and the trapping technique gave an adequate indication of the time and number of beetles attacking and of attack height. Between-tree tests were inconclusive, however, because beetle population was high; all trees, declining and healthy, were readily overcome. Approximately equal numbers of males and females were trapped at all heights (table 1). Early-attacking beetles were most numerous near the attractant bolts, about 4.2 m high. Bolt removal did not seem to influence subsequent attacks.

In the second test (upper Coastal Plain) the beetle population was limited to infested bolts placed around each test tree but was large enough that all trees, stressed or untreated, were successfully attacked. Trees were smaller than in the first test and beetles were able to produce brood with comparable ratios of increase (table 1). Turpentine beetles (*D. terebrans* [Oliv.]) also attacked the test trees and neighboring trees. An adjacent area had been clearcut earlier and turpentine beetles had developed high populations in the stumps.

1974 Tests: Results demonstrate that stressed trees can be overcome by SPB more easily than unstressed trees (table 2). Attacks were induced on the first pair of trees (1A and 1B) on 10 July 1974 and maximum OEP in these trees differed by 1 bar (5.2 vs 6.2). Available soil moisture had been virtually depleted under 1A for about 3 weeks. Tree 1B had slightly more water available on 10 July and considerably more during the pre-

Table 1. *Numbers of beetles trapped and emergence of brood from pairs of study trees (1973).*

Location	Tree pairs		Beetles trapped			Emergence	Ratio of
			Male	Female	Total	per square meter[1]	increase[2]
Lower Coastal Plain	1	Declining	2099	2013	4112	8866	9.32
		Healthy	1331	1305	2636	3691	3.91
	2	Declining	1955	1945	3900	3476	3.23
		Healthy	1592	1591	3183	5509	5.78
Upper Coastal Plain	3	Stressed	482	381	863	6682	6.73
		Control	270	239	509	2561	3.58
	4	Stressed	653	674	1327	2023	4.04
		Control	383	485	868	2755	4.27

[1] 10.76 x attacks per ft².
[2] Ratio of emerging beetles to a count of successful attacks multiplied by 2.

Table 2. *Evaluation of attacks and dates attacks were induced, bark sampled, trees cut, and bolts taken for emergence samples.*

Tree	Treatment	Attacks induced	Bark sampled	Trees cut and bolts sampled	Initial attacks	Tree response
		— — — — —	1974 dates	— — — — — —		
1A	Stressed	July 10	Aug. 7	Aug. 19	Successful	Killed by initial attacks
1B	Control	July 10	Aug. 7	Aug. 28	Unsuccessful	Succumbed after further attack
2A	Stressed	[1]	Aug. 19	Aug. 28	Successful	Killed by initial attacks
2B	Control	Sept. 4	Sept. 19	not cut	Unsuccessful	Still surviving
3A	Stressed	Sept. 4	Sept. 19	Oct. 17	Successful	Killed by initial attacks
3B	Control	Sept. 4	Sept. 19	Nov. 1	Unsuccessful	Succumbed after further attack
		— — — — —	1975 dates	— — — — — —		
4A	Stressed	July 25	Aug. 8	Sept. 3	Successful	Killed by initial attacks
4B	Control	July 25	Aug. 8	Sept. 17	Successful	Killed by initial attacks

[1] Attacks apparently initiated by parent adults that emerged from 1A.

ceding weeks (fig. 1). Prolonged periods of no or verv slow moisture depletion indicate little or no readily available water in the zone measured. Rate and quantity of water depletion depends on the intensity of tree rooting as well as on soil characteristics and atmospheric conditions.

Trees 2B, 3A, and 3B were subjected to attack on 4 September; 3A had been without significant available water since mid-June and 2B and 3B were experiencing moisture stress (fig. 1). Maximum OEP values for 2B, 3B, and 3A at that time were 7.5, 6.5, and 6.2 bars. Resin flow measurements of 20 August showed the same trend: 8.4, 5.6, and 1.6 ml. Measurements on 7 May, prior to natural or artificially induced moisture stress, yielded 8.0, 5.2, and 5.8 ml.

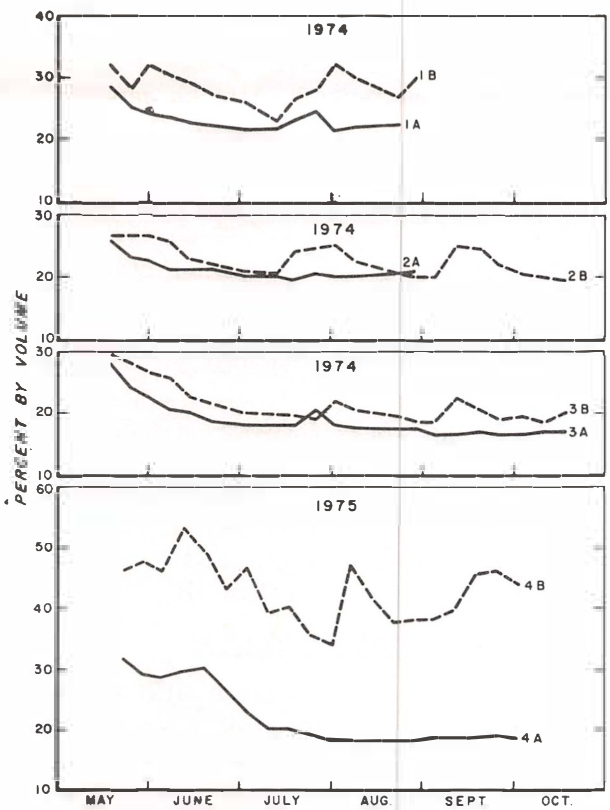

Figure 1. *Soil moisture changes under artificially stressed (solid line) and control trees (dotted line) in 1974 and 1975.*

It was apparent from periodic examination of individual attacks and from bark samples that even the beetles that attacked first met very little resistance in stressed trees (table 3). Pitch tubes were small, gallery formation and egg laying began almost immediately, and the brood reached pupal stage in about one month. Tree 2A seemed especially susceptible to attack. Unlike 1A and 3A in which attack was artificially induced, tree 2A was attacked naturally, apparently by parent adult beetles that emerged from 1A. Tree 2A was under extreme moisture stress to the extent that the crown had begun to fade and SPB attacks did not produce pitch tubes. Although the SPB apparently attacked first, large numbers of *Ips avulsus* and *I. calligraphus* also attacked the tree, especially near the 5.5 m level.

Of control trees, 2B successfully resisted all SPB attacks. No brood were produced and most attacking beetles were "pitched out" at the time bark samples were taken (table 3). The tree was also able to resist numerous black turpentine beetle attacks. SPB pitch tubes were very large compared with those on artificially stressed trees. Control trees 1B and 3B also resisted initial controlled attack but succumbed to later attacks by the SPB and *Ips* species. Observation of individual attack points and bark samples indicated that initial attacks were not successful. About one month after attack the inner bark was still wet, there were no visible signs of discoloration,

Table 3. *Status of induced SPB attacks based on bark samples and bolts cut in 1974.*

Treatment	Tree No.	Sample Height	Bark samples: Parent Adults Live	Parent Adults Dead	Larval Mines	SPB Attacks S[1]	SPB Attacks U	SPB Attacks T	Pitched Out	Dead in Gallery	Emergence from Sample Bolts
		Meters	Number per square foot [2]								
Stressed	1A	1.8	0	10	510	35	20	55	20	0	80
		3.6	0	5	500	30	5	35	5	0	51
		5.5	0	5	500	30	10	40	10	0	131
Control	1B	1.8	15	25	0	10	40	50	35	5	51
		3.6	25	45	10	15	45	60	40	5	10
		5.5	0	5	0	0	10	10	10	0	1
Stressed	2A	1.8	0	0	200	30	0	30	0	0	26
		3.6	0	0	240	40	0	40	0	0	7
		5.5	0	0	95	15	5	20	5	0	—[3]
Control	2B	1.8	0	0	0	0	15	15	15	0	0
		3.6	0	0	0	5	35	40	25	10	0
		5.5	0	0	0	5	20	25	10	10	0
Stressed	3A	1.8	55	0	230	30	0	30	0	0	214
		3.6	35	0	945	40	0	40	0	0	255
		5.5	35	0	550	35	0	35	0	0	244
Control	3B	1.8	35	0	0	20	25	45	15	10	277
		3.6	50	10	0	20	35	55	25	10	5
		5.5	55	0	0	25	20	45	20	0	1

[1] S = successful; U = unsuccessful; T = total.

[2] Multiply by 10.76 to obtain metric equivalent.

[3] No sample bolt cut; high number of *Ips* attacks and some apparent emergence.

and no larval mines were detected. However, attacks by *IPS* species and new attacks by SPB were observed. Initial beetle attacks apparently decreased resistance to subsequent attacks, but the beetles still had difficulty establishing galleries because of oleoresin flow. Two months after initial attack SPB larvae and pupae were observed.

Beetle emergence from control trees 1B and 3B was much less than from stressed trees 1A and 3A (table 3). This indicates that conditions for egg laying and brood development were not as favorable in unstressed trees.

1975 Tests: On 24 July, measurements of OEP and oleoresin flow on 4B (control) and 4A (stressed) revealed that maximum OEP was 9.6 bars in 4B and 7.9 bars in 4A. Oleoresin flow had respective figures of 5.2 and 28.4 ml. SPB attacks were induced on 25 July. At that time the stressed tree had depleted most available water in the soil and the control tree had an abundance of water (fig. 1).

For both stressed and control trees the number of induced attacks were sufficient to overcome the tree (table 4). Tree 4B apparently had a low resistance to attack regardless of water status. Recent research at Mississippi State University indicates that tree susceptibility can be predicted on the basis of oleoresin flow and other physical properties of the oleoresin system (Hodges, et al., in press). Under their system tree 4B would have been classified as highly susceptible to beetle attack. Tree 4A, previous to induced moisture stress, would have been expected to show much more resistance to attack than 4B.

DISCUSSION

First evaluations of induced SPB attacks in declining and apparently healthy trees indicated that even the most healthy loblolly pine will succumb to attack by a large SPB population. By limiting the supply of attacking beetles it was possible to demonstrate differences in resistance to attack as well as in brood production. How-

Table 4. *Status of induced SPB attacks based on bark samples and bolts cut in 1975.*

Treatment	Tree No.	Sample Height	Bark samples: Parent Adults Live	Parent Adults Dead	Larval Mines	SPB Attacks S[1]	U	T	Pitched Out	Dead in Gallery	Emergence from Sample Bolts
		Meters	Number per square foot [2]								
Stressed	4A	1.8	0	0	0	30	10	40	0	10	121
		3.6	0	0	5	30	20	50	10	10	143
		5.5	0	0	150	40	20	60	10	10	56
Control	4B	1.8	0	0	0	20	0	20	0	0	139
		3.6	0	0	0	30	10	40	0	10	32
		5.5	0	0	0	30	10	40	10	0	0

[1] S = successful; U = unsuccessful; T = total.
[2] Multiply by 10.76 to obtain metric equivalent.

ever, difficulties in selecting uniform study trees, handling beetle populations, inducing attacks, sampling bark at the correct time, rearing brood from cut bolts, and obtaining sufficient replications for analysis of variance preclude standard analysis and completely objective interpretation of results.

Several meaningful points can be made from the tests with limited SPB populations and host trees under various degrees of moisture stress. Trees under severe moisture stress (1A, 2A, 3A and 4A) have almost no resistance to attacking beetles. Although trees may yield abundant resin from a standard wound, duration of oleoresin flow is curtailed by moisture stress, and egg laying and larval development progress rapidly. Better hydrated trees hinder beetle attack primarily through oleoresin flow into the galleries. This prevents effective egg laying and larval development. Some beetles are trapped in the galleries, others are pitched out, and all must expend an unusual amount of energy.

Figures 2a and 2b illustrate the differences found between stressed and control trees at the time bark samples were taken about 2 weeks after inducing attack and when trees were felled for rearing brood (40 to 49 days after attack).

Severely stressed trees may produce a primary attractant to SPB. Beetles that attacked 2A had to bypass several non-study trees. Tree 2A produced no pitch tubes; radial growth was nil and the tree was near death at the time of attack. Such trees are perhaps similar to severely declining pines that have been observed repeatedly with SPB attacks in the mid bole. Growth has practically ceased and the oleoresin supply is negligible in such trees. If pitch tubes are produced, they are very minute.

STRESSED **CONTROL**

Figure 2a. *Exposed xylem two weeks after induced attack. Stressed tree has egg gallery etchings and blue stain; control tree has abundant oleoresin accumulation.*

STRESSED CONTROL

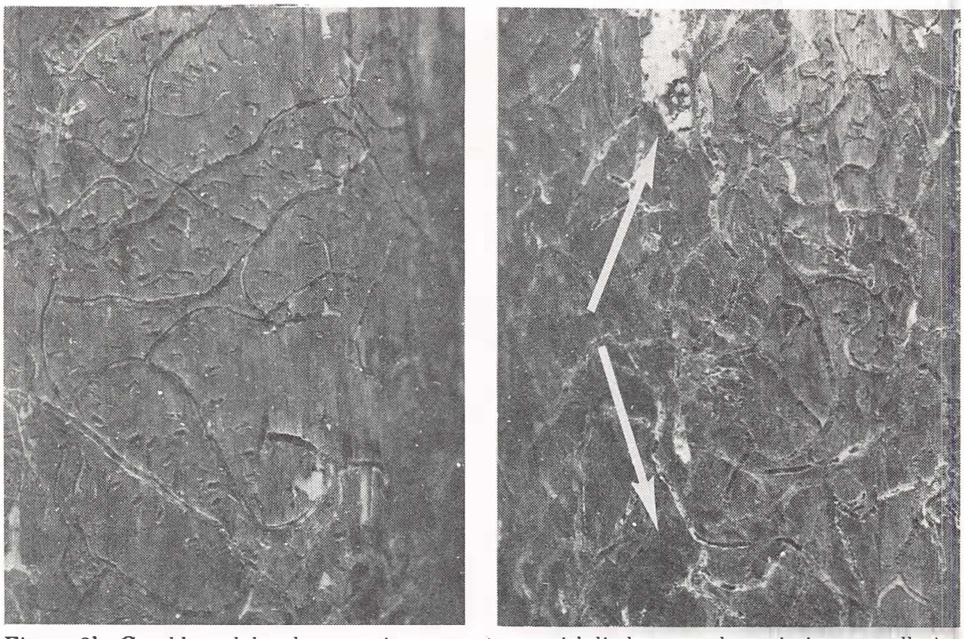

Figure 2b. *Good brood development in stressed tree with little or no oleoresin in egg galleries 40 days after induced attack. Poor brood development in untreated tree with pitch-soaked areas and oleoresin in egg galleries (note arrows) 49 days after attack.*

Trees with a moderately good water status and oleoresin supply (2B) can successfully repel a considerable SPB attack. Also, the blue stain fungus, *Ceratocystis minor,* is apparently occluded from the xylem. Pines in well-managed stands on good sites with an adequate water supply to maintain large crowns and good growth are most likely to have these oleoresin and water status characteristics.

High oleoresin flow (4A) will not necessarily deter a moderate SPB attack if an acute moisture deficit exists. Flow depends partially on the water status of the living epithelial cells surrounding the resin ducts. Internal moisture stress reduces the pressure exerted by these cells on the oleoresin, and the rate and duration of flow are curtailed.

There are various degrees of resistance to attack. Environmental conditions influence both host resistance and SPB behavior. To the extent that the environment can be manipulated, such as by thinnings and sanitation cuts, the probability of successful attacks can be reduced.

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Additional keywords: *Oleoresin exudation pressure, xylem water potential, soil moisture, resistance, susceptibility.*

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